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RESEARCH PAPER

Re-description of the Spence Shale palaeoscolecids in light of new morphological features with comments on palaeoscolecid taxonomy and taphonomy

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Abstract

The middle Cambrian (Miaolingian Series; Wuliuan Stage) Spence Shale of Utah and Idaho preserves a diverse assemblage of biomineralized and soft-bodied taxa. Among the rarest specimens of this fauna are palaeoscolecid worms. Until recently, only one specimen was known from the Spence Shale, the holotype specimen of *Palaeoscolex ratcliffei* Robison, 1969, later included in the genus *Wronascolex*. This specimen is preserved as part and counterpart but missing both the posterior and anterior terminations. A new specimen, discovered by Riley Smith, preserves an everted proboscis with spines. Based on new data collected using scanning electron microscopy and energy dispersive X-ray spectrometry (SEM–EDS), and optical microscopy, the species is thought to represent a new genus, *Utahscolex* gen. nov., rather than a species of *Palaeoscolex* or *Wronascolex* as previously suggested. The new genus differs from the other two genera in the lack of node ornamentation of the plates, as well as the absence of microplates and platelets. Based on this case study, it is recommended that future revisions of palaeoscolecid taxonomy require knowledge of plate, platelet, and microplate ornamentation, as well as the arrangement of the plates, platelets, and microplates on the cuticle. In addition to the improved morphological information provided by the new specimen, it also advances our knowledge of the taphonomic pathways in the Spence Shale and in palaeoscolecid worms in general. The preservation of the plates of the two specimens of this species differ in elemental composition and somewhat in quality. While both the holotype and new specimen show localized magnesium and phosphorus within the plates, the holotype has a substantial iron component, whereas the new specimen instead shows elevated calcium. In addition, kerogenization, pyritization, aluminosilicification, and phosphatization can be observed throughout the specimen. The preservation varies not only between the specimens, but also within, demonstrating the high variability of preservational pathways within a Burgess Shale-type deposit, and providing insights into the circumstances that lead to soft-bodied preservation in the Spence Shale.

Keywords Utah · Great basin · Priapulida · Burgess shale-type preservation · SEM–EDS

Introduction

The Cambrian (Miaolingian Series; Wuliuan Stage) Spence Shale Lagerstätte of northeastern Utah and southeastern Idaho preserves a diverse assemblage of soft-bodied and biomineralized fossils (Robison et al. 2015; Kimmig et al. 2019). While the biota is dominated by arthropods, other animals can be found. Some of the rarest fossils are palaeoscolecid worms, with only two specimens known to date.

Palaeoscolecids are Cambrian (Series 2; Stage 3) to Upper Silurian vermiform organisms included in the Ecdysozoa (Ivantsov and Wrona 2004; Maas et al. 2007; Conway Morris and Peel 2010; Harvey et al. 2010; Zhuravlev et al. 2011; Wills et al. 2012), and considered to be priapulids or

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stem-priapulids (Conway Morris 1997; Wills 1998; Huang et al. 2004a, b, 2006; Harvey et al. 2010). They are characterized by annulated cuticles ornamented with patterns of µm-scale biomineralized phosphatic plates and an armoured proboscis (Conway Morris and Robison 1986; Harvey et al. 2010). Palaeoscolecids have a near worldwide distribution and can be preserved in a variety of ways, as follows: (1) the most intact views of the palaeoscolecids are provided by compressed body fossils with soft-tissue preservation, such as by Burgess Shale-type (BST) preservation. Palaeoscolecids preserved in this manner are known from such deposits as the Burgess Shale, British, Columbia, Canada (Smith 2015); the Spence Shale, Marjum, and Weeks Lagerstätten, Utah (Robison 1969; Conway Morris and Robison 1986; Foster and Gaines 2016; Lerosey-Aubril et al. 2018; Kimmig et al. 2019); the Sirius Passet Lagerstätte, Greenland (Conway Morris and Peel 2010); the Shineton Shale, England (Whittard 1953); the Chengjiang Biota, China (Zhu et al. 2005); the Murero Shale, Spain (García-Bellido et al. 2013); the Fezouata Lagerstätte, Morocco (Martin et al. 2016; Kouraiss et al. 2018); and the Emu Bay Shale, Australia (García-Bellido et al. 2013; Paterson et al. 2016). (2) Palaeoscolecids are also known as disarticulated plates of completely organic preservation, e.g., as ‘small carbonaceous fossils’ (SCFs), from the Deadwood Formation, Saskatchewan, Canada (Butterfield and Harvey 2012). (3) Similarly, isolated calcium phosphate plates, e.g., ‘small shelly fossils’ (SSFs), of palaeoscolecids are known from such localities as the Seby Limestone, Sweden; the Parey gravel pit in Berlin Spandau-West, Germany; Clayey reddish limestone lenses in the shales on south side of Karakaya Tepe located north of Bafbaşı village, at the north of the route from Hadim to Konya, Turkey; the transitional zone between the Derenjāl and Shirgesht Formations, Iran; the Columbia Ice Fields Section, Canada; and the Galena Group and Dubuque Formation; United States (Müller 1973; Gedik 1977). Isolated palaeoscolecid calcium phosphate plates were identified independently as the microfossil form genera *Hadimopanella, Kaimenella*, and *Milaculum,* among others*;* and were only recognized as plates from palaeoscolecids beginning in 1989 (van den Boogaard 1989; Hinz et al. 1990). Last, (4) palaeoscolecids are also preserved via Orsten-type preservation, where the cuticle is secondarily phosphatized and preserved three dimensionally with plate, platelet and microplate arrangements. Palaeoscolecids preserved in this manner are known from the Mernmerma Formation, Australia (Topper et al. 2010); the middle Cambrian Georgina Basin, Australia (Müller and Hinz-Schallreuter 1993); and the Sinsk biota, Siberia (Ivantsov and Wrona 2004).

Historically, palaeoscolecids have been assigned to a variety of clades, including annelids (Whittard 1953; Robison 1969; Glaessner 1979), chaetognaths (Ahnelt 1984), nematomorphs (Hou and Bergström 1994), and nemathelminthes (Ivantsov and Wrona 2004; Maas et al. 2007). Palaeoscolecids have also been considered paraphyletic to panarthropods (Dzik and Krumbiegel 1989) or all ecdysozoans (Budd 2001), but recent literature has converged on their position within cycloneuralians, a clade of ecdysozoans consisting of scalidophorans and nematoids (Conway Morris and Peel 2010; Zhuravlev et al. 2011; Wills et al. 2012). Within that clade, there is a current consensus that palaeoscolecids represent priapulids or stem-priapulids (Conway Morris 1997; Wills 1998; Huang et al. 2004a, b; Huang et al. 2006; Harvey et al. 2010). The palaeoscolecids share their armoured proboscis with all priapulids, but phylogenetic analyses of the group are hampered by the lack of universally shared characteristics between species, and the palaeoscolecids might represent a paraphyletic group (Wills et al. 2012). Phylogenetic analyses are further complicated by the absence of phylogenetically informative characters, such as the armature arrangement and morphology of the proboscis, length/body width, presence of posterior spines, plate arrangement, and cuticular layer composition, when the specimens are not preserved as carbonaceous compressions, and even when preserved as such most specimens are missing some of this information (Wills 1998; Harvey et al. 2010; Wills et al. 2012).

The Spence Shale contains several vermiform taxa, including *Ottoia prolifica*, *Selkirkia spencei*, and *S.* cf. *columbia* (Robison et al. 2015; Kimmig et al. 2019); but *Utahscolex ratcliffei* gen. nov. represents the only known palaeoscolecid species. Originally described as *Palaeoscolex ratcliffei* Robison, 1969, it was known from a single specimen. After its first description, the holotype of *Utahscolex ratcliffei* did not receive significant interest until a revision of the genus *Palaeoscolex* in 2013 (García-Bellido et al. 2013), which suggested moving the species to the genus *Wronascolex*?, despite lacking the confirmed presence of *Hadimopanella*-type plates. Additionally, the holotype lacks any details of the posterior and anterior end, as they are both missing.

The recent discovery of a second specimen (KUMIP 490902) from the Spence Shale represents the first preservation of a proboscis in this species. Here we establish *Utahscolex* gen. nov., describe the new specimen of *Utahscolex ratcliffei*, re-describe the part and counterpart of the holotype in context of the new genus assignment, and discuss the affinity of the species, characters used in palaeoscolecid taxonomy, and the importance of taphonomy and diagenesis in the preservation of palaeoscolecids.

Geological context

Located in northeastern Utah and southeastern Idaho, the Spence Shale is the middle member of the Langston Formation, between carbonates of the overlying High Creek

Limestone and underlying Naomi Peak Limestone. The Spence Shale is assigned to the *Albertella*-*Glossopleura* trilobite biozones, and is early middle Cambrian (Miaolingian Series; Wuliuan Stage) in age (Liddell et al. 1997; Kimmig et al. 2019). It is slightly older than the Wheeler and Marjum Lagerstätten of western Utah (Drumian Stage), and the Burgess Shale (middle Wuliuan Stage) of British Columbia, Canada (Robison et al. 2015; Foster and Gaines 2016; Lerosey-Aubril et al. 2018; Kimmig 2019; Kimmig et al. 2019). The Spence Shale preserves a diverse biota of soft-bodied taxa, as well as a world-renowned assemblage of trilobites, echinoderms, and other biomineralized taxa; to date, 89 species in 72 genera have been described from this member (Robison et al. 2015; Kimmig et al. 2019; Wen et al. 2019). The Spence Shale consists of carbonate mudstones to carbonate-rich siliciclastic mudstones, with high-energy events creating sharp bases of the beds, interpreted as scours (Kimmig et al. 2019). The Spence Shale represents a middle carbonate outer detrital belt depositional setting, of a now west facing carbonate platform. The sediments record regular storm events, and abundant benthic communities during deposition of the carbonate beds and a portion of the siliclastic mudstones (Kimmig et al. 2019). The Wellsville Mountain localities (Miners Hollow, Antimony Canyon, and Cataract Canyon; Fig. 1b) were established as the most proximal environments of the Spence Shale (Liddell et al. 1997; Garson et al. 2012). However, large quantities of dolomites at the Langston Formation type locality in Blacksmith Fork, Utah, suggests it may be more proximal than the Wellsville Mountain sites (Kimmig et al. 2019). Towards the northeast, the depositional environment becomes more distal, evidenced by the decrease of dolomites and limestones, and lower abundance of soft-bodied preservation (Liddell et al. 1997; Kimmig et al. 2019). The Spence Shale is unusual for a BST deposit due to its fluctuating periods of anoxia, and association of soft-bodied preservation with zones of bioturbation (Garson et al. 2012; Kimmig and Strotz 2017; Hammersburg et al. 2018; Kimmig et al. 2019). Miners Hollow appears to be the most distal of the Wellsville Mountain localities, and contains at least six shallowing-upward cycles, or parasequences, of silty shales capped with lime mudstone or nodular lime mudstone and fossiliferous wackestone interbedded with shale (Fig. 1d; Liddell et al. 1997; Kimmig et al. 2019). The abundance of silty shale units decreases moving up section (Liddell et al. 1997; Garson et al. 2012). Miners Hollow has been one of the most studied localities of the Spence Shale, and currently has the highest diversity of soft-bodied taxa (at least 20 species; Kimmig et al. 2019).

The new specimen (KUMIP 490902) described herein was collected by Riley Smith in the scree of the carbonate-rich siliciclastic mudstones of Liddell et al.'s (1997) cycle

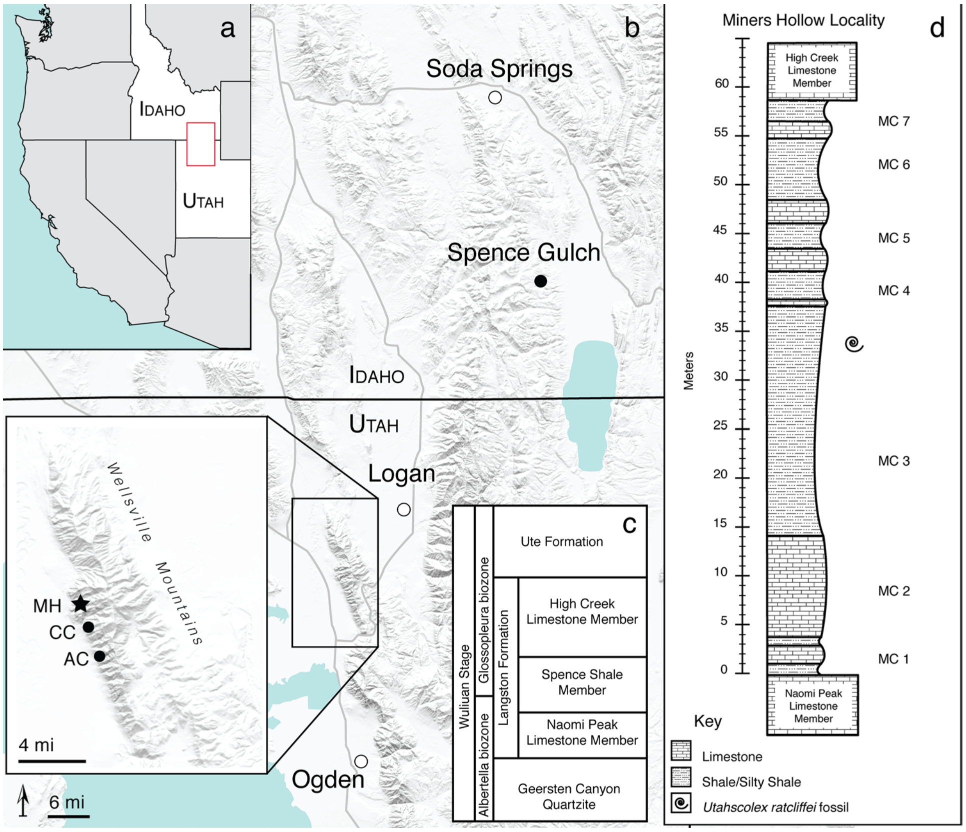


Fig. 1 Geographic and geologic setting of the Spence Shale Lagerstätte. **a** Map of the western United States showing location of the Spence Shale. **b** Topographic map (Base from U.S. Geological Survey digital data, The National Map: Terrain with Labels, accessed February 2019, at https://viewer.nationalmap.gov/basic) showing the type locality Spence Gulch, and insert showing the major Wellsville Mountain localities (*MH* Miners Hollow, *CC* Cataract Canyon, *AC* Antimony Canyon). Locality where specimens of *Utahscolex ratcliffei* were found delineated by star. **c** Simplified stratigraphy of the middle Cambrian in northeastern Utah and southeastern Idaho. **d** Stratigraphic column of the Langston Formation at Miners Hollow, showing shallowing-upward sequences and location of *U. ratcliffei* fossils, recovered from scree of cycle 3. Section measured by J. Kimmig

3 of the Miners Hollow locality in the Wellsville Mountains, Box Elder County, Utah (Fig. 1d). The holotype part (UU1020) was collected by William Ratcliffe and the counterpart (KUMIP 204390) was collected by E.F. Sorensen. The holotype also comes from the scree of cycle 3 of Miners Hollow (Robison 1969).

Methods and terminology

The morphological terminology used herein is a combination and modification of historical terms, mainly following Topper et al. (2010). Each segment of the palaeoscolecid is an 'annulus', plural 'annuli' (Topper et al. 2010; Liu et al. 2016; Martin et al. 2016; Yang and Zhang 2016). Other terms for annuli previously used are somite (Robison 1969), annulation (Conway Morris 1997) and segment (Glaessner 1979; Conway Morris 1997). The annuli are separated by an annulation boundary, previously called an interannular furrow (Topper et al. 2010), an intercalation (Conway Morris 1997), and an inter-segmental furrow (Conway Morris 1997; Yang and Zhang, 2016). The boundary between each annulus can be marked by the presence of platelets and microplates, or the notable separation of the plate rows. This annulation pattern does not necessarily indicate metameric segmentation (Conway Morris 1997; Ivantsov and Wrona 2004). In extant priapulids, the annuli structures are associated with the circular and longitudinal musculature (Vannier and Martin 2017). The presence of circular musculature in palaeoscolecids is ambiguous; circular muscle has been interpreted from several body fossils (Ivantsov and Zhuravlev 2005; Han et al. 2007), while body width uniformity and preservation in wrapped coils has been used as arguments against (Hou and Bergström 1994; Harvey et al. 2010).

Plates, platelets, and microplates are defined by expanding on the description of Topper et al. (2010), combining their relative size and relative position. Plates are defined by position as forming transverse rows on each annulus of the cuticle, and are the largest in size (Topper et al. 2010). Previous terms for plates include pits (Whittard 1953), papillae (Robison 1969; Glaessner 1979; Conway Morris and Robison 1986), tubercles (Kraft and Mergl 1989), and sclerites (Hinz et al. 1990; Hou and Bergström 1994). Ivantsov and Wrona (2004) and Ivantsov and Zhuravlev (2005) used sclerites as a general term for plates of multiple sizes observed in Siberian cuticle arrays García-Bellido et al. (2013). instead divided plates, platelets, and microplates quantitatively by diameter for *Wronascolex*, as 80–100 µm, 30–50 µm, and 15–20 µm, respectively. However, the utility of these size classes is limited within the genus, as other genera have plates, platelets, and microplates outside of these ranges, and some do not possess platelets or microplates at all.

Platelets are morphologically similar or identical to plates in miniature, and can occupy the annulation boundary as well as alternating with plates on the annulus (Topper et al. 2010). A previous term for platelets is pustules (Glaessner 1979). Microplates do not morphologically resemble the plates or platelets, but fill the space in between them and are the smallest in size. Microplates are frequently distributed in the central region of each annulus as well as in the annulation boundary (Topper et al. 2010) in some species. Nodes can be present, and are defined as the ornamentation on the surface of plates and platelets, and can vary widely in morphology, from rounded to pointed (Liu et al. 2016). Whittard (1953) referred to nodes as pores.

Terminology related to the proboscis follows Conway Morris (1977). The everted proboscis is divided into three zones (with Zone I being most proximal), potentially ornamented with hooks, plates, spines, or un-armoured zones.

Specimens were photographed under white light while immersed in ethanol using a Leica DMS 300 Digital Microscope and an Olympus SZX16 microscope. Whole specimen images were created by stitching together mosaics of smaller images using Adobe Photoshop. The colour, contrast, and brightness of the images were adjusted using Adobe Photoshop.

Specimens were examined using scanning electron microscopy (SEM), and integrated energy dispersive X-ray spectrometry (EDS). SEM imaging for KUMIP 204390 was conducted using an FEI Versa 3D Dual Beam FIB-SEM (focused ion beam not used, electron imaging only) at the University of Kansas Microscopy and Analytical Imaging Laboratory. EDS analysis for KUMIP 204390 was conducted using an Oxford Instruments 80 mm^2 x-Max silicon drift detector. Analyses conducted on this instrument used an accelerating voltage of 10 keV, a spot size of 4.5, and when available, under low vacuum conditions. SEM–EDS analyses for UU 1020 and KUMIP 490902 were conducted at the X-ray Microanalysis Core Facility at the University of Missouri, using a Zeiss Sigma 500 VP variable pressure SEM with dual, co-planar Bruker XFlash 6|30 EDS detectors (30 mm^2). Analyses were conducted with the following operating conditions: accelerating voltage of 20 keV; high current mode; working distance of 17.6 mm; variable pressure chamber vacuum at 40 Pa; and 60 µm aperture for imaging, 120 µm aperture for EDS analyses. Both a high definition 5-segment backscattered electron detector (HDBSE) and a gaseous cascade current detector (C2D) were used for backscattered (compositional) and secondary (topographic) electron imaging, respectively. EDS analyses were conducted using both detectors in tandem, thus avoiding artefacts from topography and simultaneously improving signal, which was > 150 kilocounts per second. Comparable operating conditions to those described above were previously used for analyses of vermiform Spence Shale specimens by Broce and Schiffbauer (2017).

Institutional abbreviations. KUMIP, University of Kansas Invertebrate Paleontology, Lawrence; UU, Natural History Museum of Utah, Salt Lake City.

Systematic paleontology

Phylum **Priapulida** Théel, 1906
Class **Palaeoscolecida** Conway Morris and Robison, 1986
Family **Palaeoscolecidae** Whittard, 1953

Genus ***Utahscolex*** gen. nov.

Etymology. The generic name derives from Utah, the state, where the specimens have been found.

Type species. *Utahscolex ratcliffei* Robison, 1969.

Diagnosis. As for species.

Remarks. The genus *Palaeoscolex* is characterized by bearing *Milaculum*-type plates, which are not present in the Spence Shale specimens (García-Bellido et al. 2013). *Wronascolex* is characterized by *Hadimopanella*-type plates, as well as the presence of smaller platelets and microplates, both characteristics of which are absent in *Utahscolex* (García-Bellido et al. 2013). The tentative assignment of the holotype of *Utahscolex ratcliffei* to *Wronascolex* by García-Bellido et al. (2013) was based on the potential taphonomic bias preventing the preservation of nodes on *Hadimopanella*-type plates. While the specimen presented similar size of plate diameter, annulus width, plate arrangement characteristics (the "naked zone," lacking platelets and microplates, separating the rows of plates) of *Wronascolex* Ivantsov and Zhuravlev 2005, the confirmed absence of *Hadimopanella*-type plates excludes *Utahscolex* from this genus.

The four rows of plates per annulus arranged in two bands of double rows, along with the lack of ornamented plates and the absence of microplates differentiates this genus from the genera *Austroscolex* Müller and Hinz-Schallreuter 1993, which possesses plates with 4–5 nodes and annulations with 1–2 plate rows; *Euryscolex* Müller and Hinz-Schallreuter 1993, possessing plates with a jagged outer margin and a concave upper side; *Kaloscolex* Müller and Hinz-Schallreuter 1993, possessing 1–2 plate rows per annulus and plates with 4–5 nodes; *Pantoioscolex* Müller and Hinz-Schallreuter 1993, possessing plates with 4–6 nodes and alternating rows of plates with zones of microplates; *Corallioscolex* Müller and Hinz-Schallreuter 1993, possessing 2–3 plate rows per annulus and plates ornamented with a central depression and several nodes; *Rhomboscolex* Müller and Hinz-Schallreuter 1993, possessing 2 plate rows per annulus, platelets forming a rhombic pattern in the central portion of the annulus, and plates ornamented with nodes arranged circularly around a central depression; *Schistoscolex* Müller and Hinz-Schallreuter 1993, possessing 2 rows of plates per annulus with plates ornamented with 1–4 large nodes; *Shergoldiscolex* Müller and Hinz-Schallreuter 1993, possessing 2 rows of highly ornamented plates and oval nodular microplates; *Thoracoscolex* Müller and Hinz-Schallreuter, 1993, possessing 2 rows of plates ornamented with 2–5 central nodes; and *Murrayscolex* Müller and Hinz-Schallreuter 1993, possessing 2 plate rows per annulus of alternating size, plates with a nodular upper surface, with microplates located between plates.

Utahscolex differs from *Radnorscolex* Botting et al. 2012, *Aggerscolex* Botting et al. 2012, and *Ulexiscolex* Botting et al. 2012 by the absence of ornamented plates, as well as lacking the organized patterns of platelets and microplates. *Radnorscolex* Botting et al. 2012 possesses plates with up to 12 nodes, arranged circularly; *Aggerscolex* possesses plates with nodes condensed into irregular mounds and hexagonal microplates; and *Ulexiscolex,* which possesses irregular plates with 9–13 nodes, platelets and microplates.

Compared to *Mafangscolex* Hu 2005, *Utahscolex* does not possess plates of two different sizes, ornamented with central nodes (Hou et al. 2017).

Guanduscolex Hu et al. 2008 differs from *Utahscolex* in the number of plate rows per annulus, having three, and possessing 9–10 nodes arranged around 4–5 central nodes.

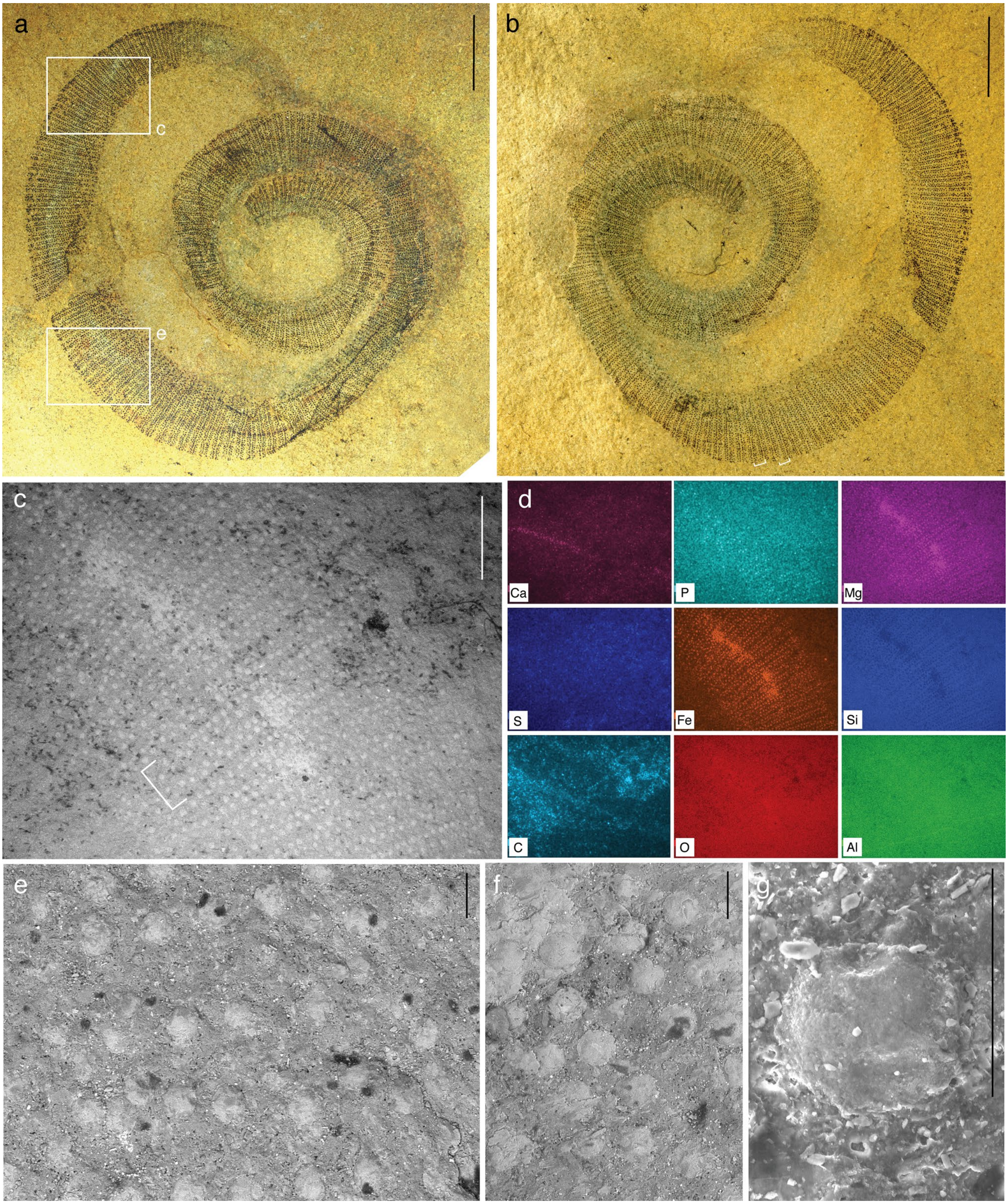
Utahscolex differs in plate ornamentation from *Yunnanoscolex* Hu et al. 2012 which possesses plates with 2–6 nodes (5 average), and *Wudingscolex* Hu et al. 2012 plates with 3 circles of nodes and platelets with 8–10 marginal nodes and 1–2 central nodes.

Utahscolex differs in plate rows per annulus and plate ornamentation from *Sanduscolex* Muir et al. 2014, which possesses plates, platelets and microplates, exhibiting ornamentation (3 + nodes on the largest size, and diminishing numbers of nodes as the plates get smaller) and *Ashetscolex* Muir et al. 2014, which has oval plates ornamented with a single line of nodes, and two plate rows per annulus.

Scathascolex Smith 2015 possesses plates with subtly-preserved fivefold symmetry reminiscent of *Hadimopanella*-type plates, the lack of *Hadimopanella* plates differentiates *Utahscolex* from *Scathascolex*.

Utahscolex ratcliffei Robison, 1969
Figures 2–3, S1–S8.

1969 *Palaeoscolex ratcliffei* sp. nov. Robison—Robison: pl. 138, figs. 1–2.
1991 *Palaeoscolex ratciffei* Robison—Robison: fig. 6.5.



2013 *Wronascolex? ratcliffei* Robison—García-Bellido et al.: figs. 9A–G.

2015 *Wronascolex? ratcliffei* Robison—Robison et al.: fig. 54.

2019 *Wronascolex? ratcliffei* Robison—Kimmig et al.: fig. 5C.

2019 *Wronascolex? ratcliffei* Robison—Kimmig: fig. 2D.

◂**Fig. 2** *Utahscolex ratcliffei* gen. nov. from the Miners Hollow locality, Spence Shale member of the Langston Formation, Utah (Miaolingian; Wuliuan). **a** Holotype part UU1020 complete specimen submerged in alcohol under oblique light. **b** Holotype counterpart KUMIP 204390 complete specimen submerged in alcohol under oblique light. Two annuli framed, showing double pairs of plate rows per annulus. Modified from García-Bellido et al. 2013. **c–g** Holotype part UU1020, **c** Enlargement of boxed inset in A, showing preserved gut tract and transverse annuli, single annulus framed, inset reflected about vertical axis from specimen. **d** SEM-EDS elemental maps of the area in **c** the plates and gut tract show enhanced levels of Fe, Mg, P, and Ca, while the host matrix show enhanced levels of K, Si, Al, and O. **e** Enlargement of boxed inset in A, showing wide unornamented zone between rows of circular plates. **f** Detail of C showing hemispherical, unornamented plates. **g** Detail of E, showing single, round unornamented plate. Scale bars represent 5 mm (**a–b**); 1 mm (**c**); and 100 µm (**e–g**)

Holotype. Part (UU1020) and counterpart (KUMIP 204390), Spence Shale Member, Langston Formation, Utah, USA.

Other material. KUMIP 490902.

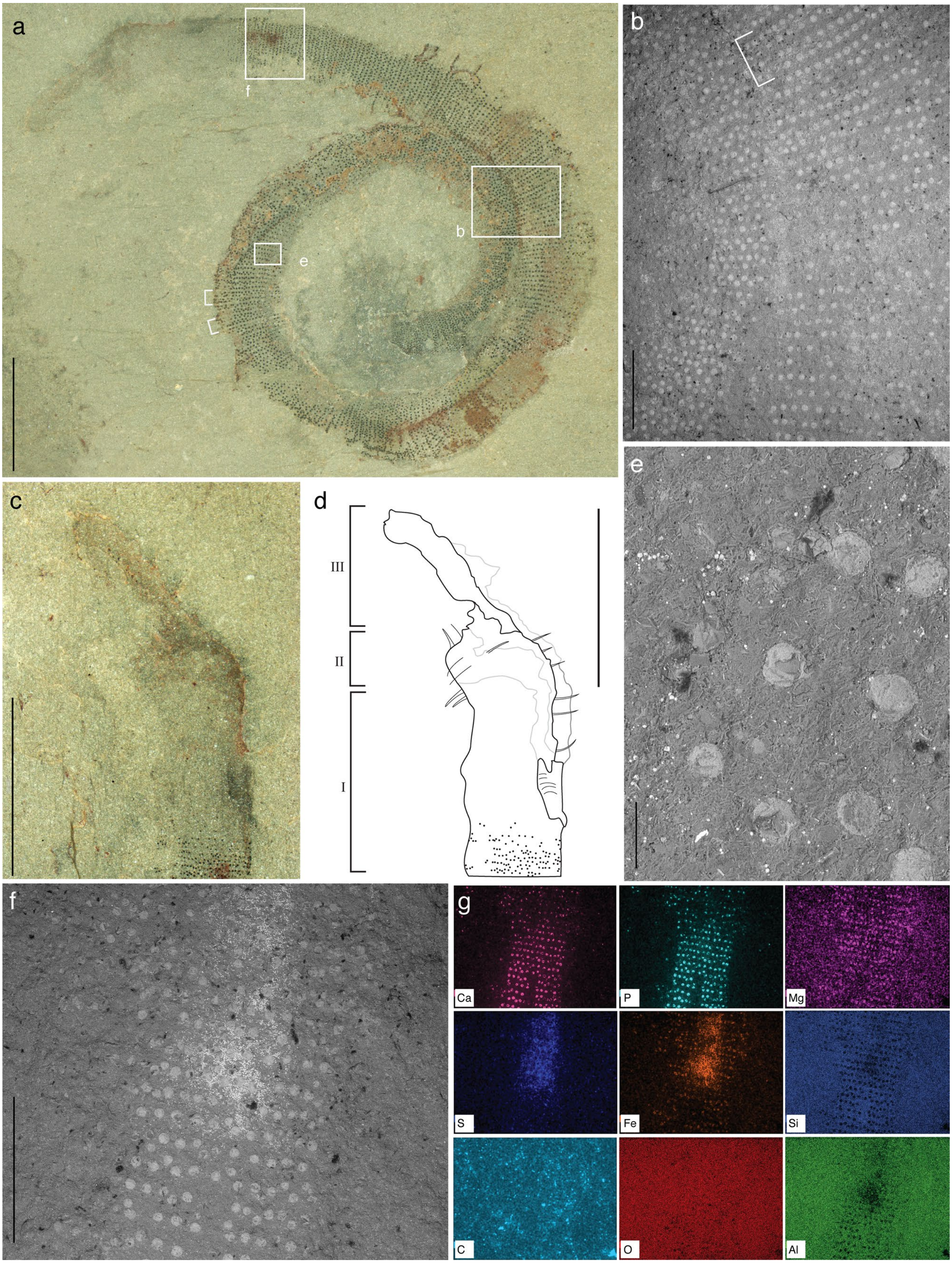
Emended Diagnosis. 1–3 annuli per mm, with more annuli/mm at the anterior and posterior terminations of the specimens. 4 transverse rings of plates per annulus, arranged as two 'bands' of double rows of plates separated by a central naked zone. Occasionally, single row bifurcates into to two rows (for up to 6 rows per annulus). Plates are circular, and unornamented. Platelets and microplates absent. Eversible proboscis with spines, gut simple and straight. Posterior end not preserved. (Modified from García-Bellido et al. 2013).

Occurrence. Spence Shale Member, Langston Formation, cycle 3, Cambrian (Miaolingian; Wuliuan), *Glossopleura* trilobite zone. Holotype specimen UU1020/KUMIP 204390 and the new specimen KUMIP 490902 were collected from the talus slope between 13 and 37 m; SE ¼ Sec. 14, T. 10N., R. 2W., Miners Hollow locality, near Calls Fort, Wellsville Mountains, Box Elder County, Utah, USA.

Description. The fossils are preserved as two-dimensional compressions, tightly coiled. The holotype specimen (UU1020 and counterpart KUMIP 204390) has a width of 2.5 mm to 4.0 mm at its widest. The new specimen (KUMIP 490902), is slightly smaller, with a width ranging from 1.6 mm to 3.5 mm at its widest. Plates are circular, ranging from 68–82 µm in diameter on UU1020 and counterpart KUMIP 204390, and 55–70 µm in diameter on KUMIP 490902. Platelets, traditionally defined by their similar ornamentation to plates and presence between plates, are not present. Microplates are not present. Annuli are defined by the thinner and more organized boundary of adjoining annuli; with the naked zone separating the double bands within an annulation being wider and less organized. Specimens range from 75 mm (KUMIP 490902) to 110 mm (UU1020, KUMIP 204390) in length if straightened. The smaller specimen, KUMIP 490902, represents a juvenile or sub-adult of the species. Neither the holotype part and counterpart (UU1020, KUMIP 204390), nor KUMIP 490902 show the posterior termination; specimen KUMIP 490902 preserves the anterior termination with everted proboscis. In KUMIP 490902 the proboscis is fully extended, in eversion stage 4 of Conway Morris (1977), displaying all 3 zones. Large oral spines are outlined on the introvert near the everted pharynx, but details of their morphology, or smaller scalids, are not present (Fig. 3c, d). The holotype part (UU1020) and counterpart (KUMIP 204390) demonstrate different cuticle arrangements, appearing as non-identical 'wrinkles' of the annulations, most notably on the outer coil. Robison (1969) suggested these differences were due to the plane of compression splitting within the thickness of the fossil.

Remarks. Compared to the proboscis of *Palaeoscolex*? *sinensis* Hou and Bergström, 1994, *U. ratcliffei* lacks the prominent oral spines and overall inflated shape. The proboscis of *U. ratcliffei* does not show any characteristics of pharyngeal teeth, as described from the lower Ordovician *Palaeoscolex* cf. *tenensis* from the Fezouata Shale (Kouraiss et al. 2018). Lack of oral spines and scalids on the proboscis may be due to preservation, but the presence of the delicate structure of the pharynx suggests near optimal preservation conditions. The proboscis of *Wronascolex*? sp. 1 described by García-Bellido et al. (2013) is in stage 2 of eversion of Conway Morris, and has short, fine, oral spines, which are not shown in *U. ratcliffei*. Compared to the proboscis of *Scathascolex minor* Smith 2015, *U. ratcliffei* shares the spines between Zones I and II, but lacks the clearly defined anterior-facing pharyngeal 'teeth' (Zone III) seen in *S. minor*. *Utahscolex ratcliffei* shares a similar plate arrangement to *S. minor*, which also has 4 plate rows per annulus, arranged in double bands of two rows.

The material assigned to *U. ratcliffei* from the Murero Shale (Miaolingian Series, Wuliuan Stage) of Spain, the Kaili Biota of China and the Lampazar Formation of Argentina has been excluded from this identification, based on the incompleteness of detailed plate ornamentation information (Conway Morris and Robison 1986; García-Bellido and Aceñolaza 2005, 2011). The material described by García-Bellido and Aceñolaza (2005) preserves a tessellated pattern reminiscent of palaeoscolecid material (Harvey et al. 2010), but does not preserve biomineralized plates. The lack of plates and incompleteness of the specimen renders diagnosis to genus or species level currently impossible. While the specimen of *Palaeoscolex* cf. *ratcliffei* described by Conway Morris and Robison (1986) from Spain shares nominal plate arrangement similarities with *U. ratcliffei*, the association was tentative based on the presence of the 'unornamented zone' between the plate rows, which distinguished


a
f
b
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b
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III
II
I
e
f
g
Ca
P
Mg
S
Fe
Si
C
O
Al

◂**Fig. 3** **a**–**f** New specimen of *U. ratcliffei* (KUMIP 490902) from the Miners Hollow locality, Spence Shale member of the Langston formation, Utah (Miaolingian; Wuliuan). **a** Complete specimen submerged in alcohol under oblique light. Two annuli framed, showing double pairs of plate rows, with examples of a single row bifurcating into double row. **b** Enlargement of inset in **a** showing creased area between the inner and outer coil of the worm, and rows of plates. Single annulus is framed, showing double pairs of plate rows. **c** Everted proboscis showing stage 4 eversion of Conway Morris (1977). **d** Line drawing of proboscis with 3 zones of Conway Morris (1977), with large proboscis spines between Zones I and II, and long unarmed length ending in a slightly bulbous tip (Zone III). **e** Enlargement of inset in **a** showing unornamented, round plates and absence of platelets or microplates. **f** Enlargement of inset in **a** showing plate arrangement and patches of framboidal pyrite (light areas near center). **g** SEM–EDS elemental maps of the area in **f** plates show elevated levels of Ca, P, Mg, and Fe, while the host matrix shows elevated levels of Si, K, O and Al. The pyrite framboids appear in the Fe and S maps. Scale bars represent 5 mm (**a**, **c**, **d**); 1 mm (**b**, **f**); and 100 µm (**e**)

it from the other two contemporary species of comparison *Palaeoscolex piscatorum* and *Palaeoscolex antiquus*. However, the lack of further information on the details of the plates, platelets, and microplates makes further comparison impossible, and this material is also excluded from this identification.

A palaeoscolecid worm from the early Middle Cambrian of Guizhou, China was tentatively identified as *Palaeoscolex* cf. *ratcliffei* (GTBM-9-1-779) preserving the anterior termination and partial posterior termination (Zhao et al. 2005). However, this specimen was not described, and there is no information on the plates, platelets or microplate arrangement. Therefore, this material is left in open nomenclature (sensu Bengtson 1988) within the palaeoscolecids. Excluding these specimens restricts *U. ratcliffei* to Laurentia.

Results

Specimens UU1020, KUMIP 204390, and KUMIP 490902 feature multiple modes of preservation, including kerogenization, phosphatization, pyritization, and aluminosilification (Figs. 2d, 3g). The plates of the holotype specimen UU1020 and KUMIP 204390 are preserved predominantly as iron–magnesium oxides. Some of the plates are preserved as calcium phosphate, but the presence of these elements varies by position across the specimen (Fig. 2d, Suppl. S5–S8). The gut tract is viewed as a dark grey or reflective band under oblique light, found in the middle of the specimen near the anterior end, and shifting towards the inner wall of the coils towards the posterior termination. It is preserved as an iron–magnesium oxide. Carbon is present predominantly in the form of small kerogen flakes, seen in SEM backscattered electron images as dark grey to almost black patches. These flakes are scattered throughout the worm, and concentrated on the outer edges of the specimen. EDS elemental mapping of KUMIP 204390 confirms the visible conclusion it is the counterpart to UU 1020, as they share highly comparable elemental composition of the fossil and host matrix.

The preservation of KUMIP 490902 differs in plate preservation from the holotype specimen. The plates are preserved primarily as calcium–magnesium–phosphate (Fig. 3g). Visible reddish patches of the fossil represent clusters of framboidal pyrite and iron oxide weathering products, hemispherical and about 5.0 µm in diameter. They replicate the gut, sometimes fill the spaces between plates, and can slightly obscure the edges of the plates. The pyritized patches are found predominantly extending from the borders of the specimen, and occasionally replicate details of the annuli. Like the holotype, kerogen appears as small, darkened flakes throughout the specimen. The concentrated kerogen mimics the boundaries of the specimen and annulations, forming an outline. The proboscis of the specimen is preserved mainly through aluminosilification, appearing as a darkened outline. The outer edge of the proboscis is distinguished as a reddish border, with the darker aluminosilification outline extending beyond the sharp boundary. The composition of the fossil preserved through clay minerals and the host matrix do not differ as strongly, which corroborates similar vermiform preservation from the Great Basin (Broce and Schiffbauer 2017).

Discussion

Taphonomy

Following suit with the generally accepted requisites for Burgess Shale-type preservation (e.g., Gaines 2014), the two *U. ratcliffei* specimens analysed here indicate having undergone rapid burial into likely anoxic or at least low-oxygen conditions (Garson et al. 2012) and early cessation of postmortem decay. This interpretation is largely based on the preservation of relatively labile features, including the proboscis, most of the gut, and little indication of decay of the worm itself. KUMIP 490902 spent comparatively more time decaying before being buried than the holotype, evidenced by the uneven and sometimes incoherent outer boundary of the specimen. The holotype (UU1020 and KUMIP 204390) does not show signs of any major biological information loss through decay. Both slabs of the holotype, as well as the slab preserving the new specimen, are very fragile, and thus no preparation was attempted.

Interpretations of the level of decay experienced by the Cambrian priapulid *Ottoia prolifica* suggest that gut and internal organs become visible after slight decay (Conway Morris 1977), and can preserve a robust record of diet if gut contents are identifiable (Vannier 2012). In specimens presumed to illustrate more advanced decay, however, the proboscis is usually everted and nearly detached from the remaining cuticle (Conway Morris 1977). Laboratory-based decay experimentation of the modern priapulid *Priapulus caudatus* showed that labile, non-cuticular features, such as the gut, begin decaying immediately following death, and are lost in under a week of decay (Sansom 2016). In contrast, recalcitrant, cuticular features were more robust and retained anatomical details for longer in the decay process (Sansom 2016). The presence and attachment of the proboscis and preservation of the gut tract in specimen KUMIP 490902 thus indicates that this specimen underwent minimal decay. Consequently, the absence of plate ornamentation or microplates is most likely not attributable to taphonomic loss, as they represent robust characteristics that would probably preserve, if present.

The soft tissue of both specimens of *U. ratcliffei* is preserved as a combination of kerogenization and aluminosilification (Figs. 2d, 3g). In the holotype (UU1020 and KUMIP 204390), the gut has been partially replaced by iron–magnesium oxides, likely a weathering product of original pyritization, while the plates are primarily preserved as iron–magnesium–phosphate. In contrast, the plates in the new specimen (KUMIP 490902) are preserved calcium–magnesium–phosphate, and the gut preserved as pyrite, similar to older guts from the Ediacaran (Schiffbauer et al. 2020) as well as other Cambrian examples (Zhu et al. 2014). The preservation of the plates in both specimens indicates an original phosphatic composition, as has been suggested for palaeoscolecids in the past (Müller and Hinz-Schallreuter 1993; Harvey et al. 2010; Kouraiss et al. 2018). Both specimens preserve large amounts of calcium-magnesium association throughout the specimen, and partially the host rock, likely indicating diagenetic dolomitization.

The confluence of differing mineralization pathways, whether taphonomically active or not, within broader Burgess Shale-type preservation is not a new concept (e.g., Gabbott 1998; Orr et al. 1998; Gabbott et al. 2004; Lin and Briggs 2010; Anderson et al. 2011; Schiffbauer et al. 2014; among numerous others), and is also known from previous studies on the Spence Shale. For instance, Broce and Schiffbauer (2017) found vermiform taxa preserved by phosphatization, aluminosilification, pyrite association, and kerogenization from the Spence Shale at Miners Hollow and Antimony Canyon. Other analyses (unpublished data) found aluminosilification, pyrite association, kerogenization, and ferro-dolomite in soft-bodied taxa from the Spence Shale at Miners Hollow. These studies, together with the data presented herein indicate that the preservation of the soft-bodied taxa in the Spence Shale underwent several stages, and the presence of dolomite and ferro-dolomite indicate diagenetic overprint. The variability of the taphonomic pathways and diagenetic signatures within one cycle of one locality of the Spence Shale shows that future work is needed to understand preservation pathways and diagenetic history within the Spence Shale as a whole. This is critical to consider, because the Spence Shale has previously been regarded as a preferable geologic setting to model Burgess Shale-type preservation, as compared to units such as the Burgess Shale and Maotianshan Shale, which have been altered by greenschist facies metamorphism and intensive subsurface weathering, respectively (Gaines et al. 2008). The high variability in these initial taphonomic studies of the Spence Shale suggest this is not valid.

Taxonomy

The use of morphological plate type (as presence/absence) is a recent taxonomic approach attempting to unify the variable preservational modes of palaeoscolecids (Ivantsov and Zhuravlev 2005; García-Bellido et al. 2013). García-Bellido et al. (2013) revised the genera *Palaeoscolex* and *Wronascolex*, dividing the taxa among the two based on the presence of *Milaculum*- or *Hadimopanella*-type plates, respectively. *Hadimopanella*-type plates are circular, with a ring of 3–10 nodes and occasional central node (García-Bellido et al. 2013). However, plate morphology can vary with position, and multiple types of plates can be represented on individual specimens (Müller and Hinz-Schallreuter 1993; Ivantsov and Wrona 2004; Topper et al. 2010). In addition little is known about ontogenetic variation in palaeoscolicid plates. Ventral and dorsal differences in plate morphologies and annulations have been noted, potentially representing functional adaptations for mobility through substrate (Müller and Hinz-Schallreuter 1993; Ivantsov and Wrona 2004). On the specimen level, scleritomes recovered from the South Australian Mernmerna Formation show multiple *Hadimopanella* form species on the same individual (Topper et al. 2010). The taxonomic validity of isolated palaeoscolecid plates is ambiguous, as there is wide range of characters within form genera and species. Topper et al. (2010) discussed the variability within the *Hadimopanella* genus, which has 14 form species, differentiated by the minute differences in node orientation, size, number, and spacing. Even on the species level, assemblages of isolated plates assigned to the form species *Hadimopanella oezgueli* varied in number of nodes from 2 to 15, with several of the larger plates bearing a striking resemblance to the oblique, lined node plates of *Milaculum* (Wrona and Hamdi 2001). Due to the variation of plate morphologies within specimens, variation of plates within a single genus or even species, and the potential for convergence of form, it is problematic to taxonomically differentiate palaeoscolecids based on presence or absence of morphological plate type.

Utahscolex ratcliffei was tentatively assigned to the genus *Wronascolex* by García-Bellido et al. (2013), despite not locating *Hadimopanella*-type plates. The preservation of the plates as iron–magnesium oxide on the holotype counterpart (KUMIP 204390) was hypothesized to prevent the preservation of potential nodes, thus *U. ratcliffei* was tentatively included in the genus (García-Bellido et al. 2013).

Analysis and comparison of the new specimen (KUMIP 490902) of *U. ratcliffei* and the holotype part and counterpart (UU1020 and KUMIP 204390) show variations in preservation of the plates. The plate preservation of *U. ratcliffei* holotype part counterpart UU1020 and KUMIP 204390 is dominated by high concentrations of magnesium and iron, with locally elevated phosphate and calcium levels, while the plate preservation of the new *U. ratcliffei* specimen (KUMIP 490902) is dominated by high, concurrent concentrations of calcium, phosphate, magnesium, and iron. While the plates of both specimens are diagenetically altered from their original preservation, there was no evidence to suggest the change would result in the complete loss of plate ornamentation, as they are robust characteristics, and other details (such as proboscis spines) were preserved. Despite multiple points of analysis across the specimen and variation in preservation, no plate ornamentation, platelets, or microplates were located. Therefore, a taphonomic bias restricting their preservation is unlikely, and these characteristics can be attributed to true absences.

It is clear from the re-evaluation of *U. ratcliffei* our current knowledge of palaeoscolecid characteristics requires increased analytical detail to determine whether absence of characters are true absences, or the result of preservational or taphonomic bias. Topper et al. (2010) required multiple complete specimens, or large sections of cuticle scleritome, to eliminate intraspecific and ontogenetic variation when conservatively establishing a new taxon. Botting et al. (2012) reached a similar consensus, considering the presence of plates and microplates, with plate and interplate structure, the minimum preservation requirements to describe a new species. In the case of *Utahscolex*, the presence of two nearly complete compression specimens, one with an anterior termination, that preserve plates and cuticle arrangement, and re-examination for potential plate ornamentation, meets the criteria for conservatively establishing a new genus. In the future, to make taxonomic revisions of the palaeoscolecids, best practices would include having at least a large (multiple annuli) section of cuticle scleritome, analysed under SEM with EDS. Plate, platelet, and microplate arrangement are needed, as well as the node morphologies of the plates and platelets. Due to inter-specimen preservation variation, multiple points of comparison are needed across the specimen. Ideally the proboscis and posterior terminations should also be present.

Conclusion

The palaeoscolecid worms of the Spence Shale, though few in number, provide valuable insight to the ongoing issues regarding the taxonomic characters of palaeoscolecids, as well as adding to the understanding of the complex taphonomic pathways of the Spence Shale. *Utahscolex ratcliffei* adds to the soft-bodied record of the Spence Shale, demonstrating the potential for exquisite preservation in unconventional BST deposit conditions. The multiple modes of preservation between specimens represent the inter-locality variations on a larger BST preservation process. Minute differences in microenvironments can create preservation differences within specimens, which is critical to know for palaeoscolecid taxonomic work that depends on the preservation of sections of plate, platelet, and microplate arrangement. The creation of *Utahscolex* represents a second genus of palaeoscolecid within Laurentia that lacks platelets and microplates, adding to *Scathascolex* from the Burgess Shale. The presence of arrangements of multiple-sized plates, platelets, and microplates has been a primary trait of palaeoscolecids historically, but the presence of multiple specimens lacking these fundamental characteristics may force a re-assessment of the taxonomy of palaeoscolecids, which has previously hypothesized to be paraphyletic (Harvey et al. 2010). The solution to the unity of the palaeoscolecid body fossil and isolated plate record is still unresolved, as the variation of plate taxonomy renders diagnostic features ineffectual.

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